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ON THE SKELETO-MUSCULAR MECHANISMS OF THE ANTERIOR ABDOMINAL SEGMENTS OF CERTAIN ADULT HYMENOPTERA

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With 11 Text-figures

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I. Introduction

The most striking structural feature of the Hymenoptera Apocrita is the fusion of the first abdominal segment with the metathorax and the constriction of the second abdominal segment to form a petiole. Snodgrass (1942) has pointed out that, whereas in the more generalised insects the abdomen is moved by dorsal and ventral intersegmental muscles, in most winged insects (fig. 1A) the dorsal intersegmental muscles of the metathorax (*d3*) have become part of the flight mechanism with the transfer of the phragma of their abdominal attachment to the thorax. As a result there are no dorsal motor muscles between the thorax and the abdomen, ventral muscles are poorly developed and there is little mobility between the thorax and abdomen. In the Hymenoptera Apocrita the dorsal and ventral muscles of the first abdominal segment (which is fused with the metathorax) act as dorsal and ventral motor muscles of the rest of the abdomen (fig. 1B), and the constriction of the anterior part of the second abdominal segment gives the high degree of mobility to the abdomen which is so characteristic of this group of insects when using the ovipositor or sting. This mobility might also facilitate displacement movements of the abdomen in the regulation of flight. It is unfortunate that little

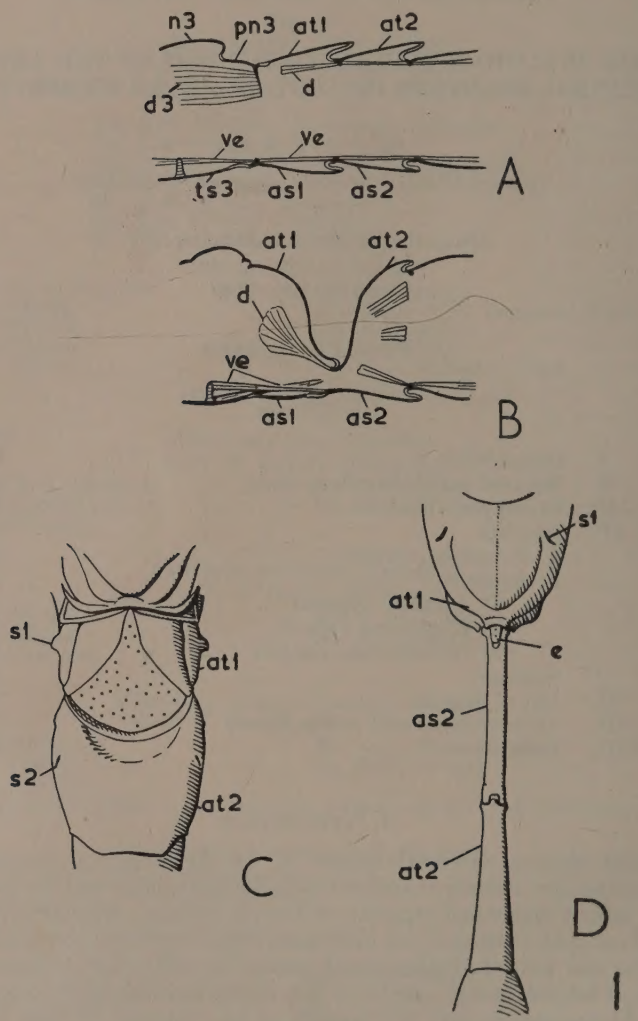

FIG. 1.—A. Diagram of thoracico-abdominal relation in a generalised winged insect: the dorsal intersegmental muscles (*d3*) are wing motors and do not move the abdomen. (*After Snodgrass, 1942.*)

B. Specialised condition of abdomen in clistogastrous Hymenoptera: dorsal (*d*) and ventral (*ve*) muscles of first abdominal segment (propodeum) have become effective motors of rest of abdomen. (*After Snodgrass, 1942.*)

C. Dorsal view of anterior part of abdomen in a Cephoid (*Calameuta pallipes* (Klug.)).

D. Dorsal view of anterior part of abdomen in a Sphecoid (*Ammophila sabulosa* (L.)).

(For explanation of lettering on this and subsequent figures, see p. 202.)

is known on this subject (Pringle, 1957). A further mechanical advantage, also noted by Snodgrass, is that the dorsal wing muscles of the mesothorax are able to acquire increased length by the extension of the mesothoracic postphragma into the first abdominal segment (see fig. 6D, *2ph*).

This fusion of the first abdominal segment with the thorax may be observed during the prepupal and pupal stages of the Hymenoptera Apocrita—see, for example, the sequence of illustrations given by Heslop-Harrison (1958 : fig. 3).

In the Hymenoptera Symphyta these specialisations of the abdomen are absent and the condition of the skeleton and dorsal muscles is similar to that shown in figure 1A, although in the Cephidae, which are thought to link the Symphyta to the Apocrita (Ross, 1936, 1937), there is a constriction between the first and second abdominal segments (fig. 1C) which gives a first indication of the condition in the Apocrita (see also Richards, 1956 : fig. 29). In the Apocrita, as will be shown in this account, the anterior abdominal segments have a general basic pattern with various specialisations in the different groups—see, for example, figure 1D of the very long petiole of the Sphecid *Ammophila*, where the second abdominal tergum has moved posteriorly and fused ventrally, and the second abdominal sternum has moved anteriorly and fused dorsally. It would appear, from the appearance of the external skeleton, that this modified sternum has produced parts for articulation with the first abdominal segment and for muscle attachment very similar to those of the second abdominal tergum of other Apocrita.

The purpose of this study is to examine the basic condition of the anterior abdominal segments in a member of the Symphyta and to compare this condition with that of certain Apocrita, these being selected so as to give some representation of the major groups of this suborder. *Urocerus* was selected as an example of the Symphyta, and, of the Apocrita, *Rhyssa* as an example of the Parasitica, and *Bombus*, *Vespula* and *Dorylus* of the Aculeata. Differences between the sexes in the musculature of the anterior part of the abdomen are relatively slight, and males of *Dorylus* have been compared with females of the other Hymenoptera studied.

The nomenclature of the Symphyta examined is that given by Benson (1951), and of the Apocrita that given by Kloet and Hincks (1945). The terminology used for the muscles is that of Snodgrass (1931, 1935, 1942, 1956). In the figures illustrating this account the standard convention of using stipple to indicate membrane has been followed.

II. Material and Acknowledgments

The dissections illustrated were made from alcohol-fixed material under a Cook, Troughton and Simms stereoscopic microscope, the dissections being illuminated by a Beck Tenslite lamp.

I wish to thank Mr. K. H. Ooi for sending me material of *Dorylus* from West Africa, and Dr. I. H. H. Yarrow for identifying this material. I am most grateful to Dr. R. E. Snodgrass for his kind permission to reproduce two figures from his paper of 1942.

I also wish to thank the Carnegie Trust for the Universities of Scotland and the University of Aberdeen for grants covering the cost of the illustrations in this paper.

III. Symphyta

The First Two Abdominal Segments of the Female of Urocerus gigas gigas (*L.*). (*Figs.* 2, 3)

The first abdominal segment is specialised. It cannot correctly be called a propodeum, since this term refers to the condition in the Apocrita where the first abdominal segment is intimately fused with the metathorax and forms anatomically a part of the thorax (Snodgrass, 1935 : 192), but the dorsal part of the first abdominal tergum (fig. 2, *at1*) is fused with the metathoracic tergum (*mt*), and there is no clear line of membrane between these parts as in generalised insects.[1] Also the first abdominal tergum possesses a tongue-like projection (*t*), which fits beneath the metathoracic epimeron (*ep*) and interlocks there. The musculature, too, provides evidence of some degree of union between the first abdominal segment and the metathorax, since the muscles numbered 8, which have origin on the second abdominal sternum (*as2*), insert on the coxae of the hind legs (*mc*). The first abdominal tergum is moderately convex in form and is split in the mid-dorsal line. The spiracles (*s1*) are lateral in position on the tergum and have an internal closing apparatus. The sternum of the first abdominal segment (*as1*) is reduced to a thin, lightly-sclerotised strip anterior to the median part of the second abdominal sternum. This is a condition similar to that found in most Apocrita.

The muscles of the first abdominal segment are as follows (fig. 2c, d, e):—

External dorsal muscles (*1*) *having origin on the posterior part of the tergum of the first abdominal segment and insertion on the antecosta* (act2) *of the second abdominal tergum* (at2).—These thin, flat plates of muscles show a reversed position. They function as extensors, since their contraction protracts the segmental plates by reducing the overlap between them. The position of these muscles contrasts with that of the corresponding muscles (9) in the second abdominal segment, where the point of origin is more median and the point of insertion more lateral. Since both of these pairs of muscles run obliquely, they can produce a movement of partial torsion.

Median internal dorsal muscles (*2*) *having origin on the antecosta of the first abdominal tergum and insertion on the antecosta of the second abdominal tergum.*—These thin, flat plates of muscles are tergal retractors since their contraction retracts individual tergal plates.

[1] In this account the antecosta and acrotergite (Snodgrass, 1935 : 252) of the first abdominal tergum which, as in all winged insects, are fused with the metathorax, are regarded as part of the metathorax and excluded from study.

Fig. 2.—*Urocerus gigas gigas* (L.) female.

a. Lateral view of metathorax and anterior abdominal segments with metathoracic coxa removed.

b. Lateral view of median longitudinal section of skeleton of metathorax and anterior abdominal segments. The cross hatching on the metathoracic endosternum represents a cut region.

c. Dorsal view of dissection of first abdominal segment.

d. Lateral view of dissection of first abdominal segment.

e. Dorsal view of dissection, showing part of metathoracic endosternum, the first abdominal sternum and the anterior part of the second abdominal sternum.

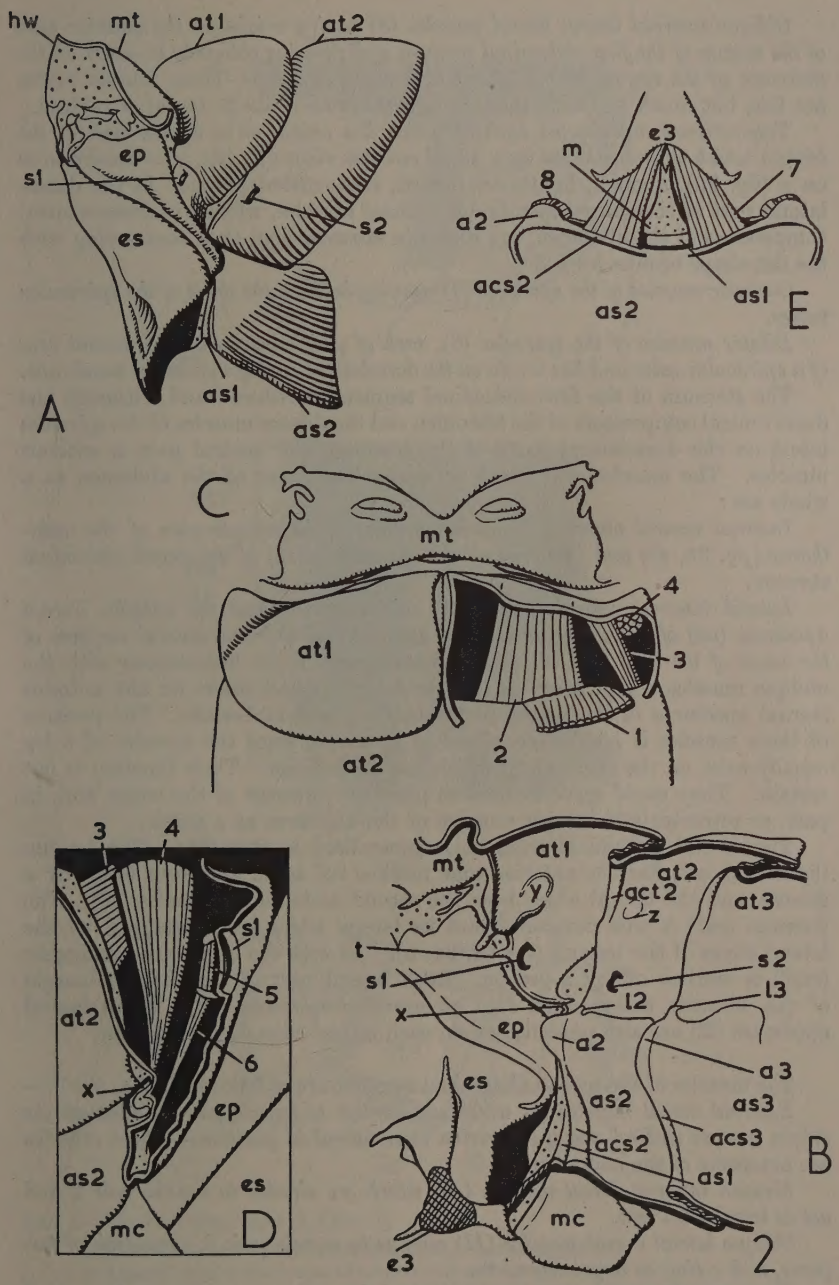

FIG. 2.—*Urocerus gigas gigas* (L.) female.

Oblique internal lateral dorsal muscles (*3*) *having origin on the anterior part of the tergum of the first abdominal segment and running obliquely to insert on the antecosta of the tergum of the second abdominal segment.*—These muscle plates are flat, but much less wide than 2. They are also, like 2, tergal retractors.

Tergo-sternal muscles (*4*), *each of which has origin on a lateral part of the tergum which is strengthened by a small circular ridge* (*fig.* 2B, y).—Insertion is on *x* (fig. 2D), a small, lightly-sclerotised, crescentic depression in the dorso-lateral part of the sternal membrane. These muscles, which are dorso-ventral compressors of the abdomen, are round in cross-section, thus contrasting with the flat shape of muscles 1–3.

Occlusor muscles of the spiracles (*5*) *running between the arms of the spiracular valves.*

Dilator muscles of the spiracles (*6*), *each of which inserts on the ventral arm of a spiracular valve and has origin on the dorsolateral part of the sternal membrane.*

The sternum of the first abdominal segment is reduced and, although the dorsoventral compressors of the abdomen and the dilator muscles of the spiracles insert on the dorsolateral parts of the sternum, the ventral part is without muscles. The muscles which act as sternal retractors of the abdomen as a whole are :

Internal ventral muscles (*7*) *having origin on the endosternum of the meta-thorax* (*fig.* 2E, e3) *and insertion on the antecosta* (acs2) *of the second abdominal sternum.*

Lateral internal ventral muscles (*8*) *which run between the anterior sternal apodemes* (a2) *of the second abdominal segment and the ventrolateral surfaces of the coxae of the hind legs.*—These muscles appear to be homologous with the oblique muscles which arise on the metasternum and insert on the anterior sternal apodemes of the second abdominal segment in *Locusta*. The position of these muscles is highly specialised in *Urocerus*, since the muscles of a leg usually arise on the segment to which the leg belongs. Their function is not certain. They could serve in part as promotor muscles of the coxae and, in part, as retractor and levator muscles of the abdomen as a whole.

The second abdominal segment is generalised in structure. The tergum (fig. 2A, B, *at2*) has the anterior edge marked off as an antecosta (*act2*) by a groove, and the lateral edges bear the second abdominal spiracles (*s2*). The sternum (*as2*) is well developed and its lateral edges are overlapped by the lateral edges of the tergum (see fig. 2A, B). As with the tergum, an antecosta (*acs2*) is marked off by a groove. Each lateral part of the anterior margin of the sternum is expanded into an anterior apodeme (*a2*). Small lateral apodemes (*l2*) are also present, one on each lateral edge of the sternum.

The muscles of the second abdominal segment are as follows (fig. 3A, B, C) :—

External dorsal muscles (*9*) *which are similar to muscle pair 1, although the origin is more median and the insertion more lateral in position.*—These muscles are extensors of the abdomen.

Median internal dorsal muscles (*10*) *which are similar to muscle pair 2 and act as tergal retractors.*

Oblique lateral dorsal muscles (*11*) *similar to muscle pair 3, consisting of two parts, and acting as tergal retractors.*

Tergo-sternal muscles (*12*), *each of which has origin on* z (*fig.* 2B), *a small*

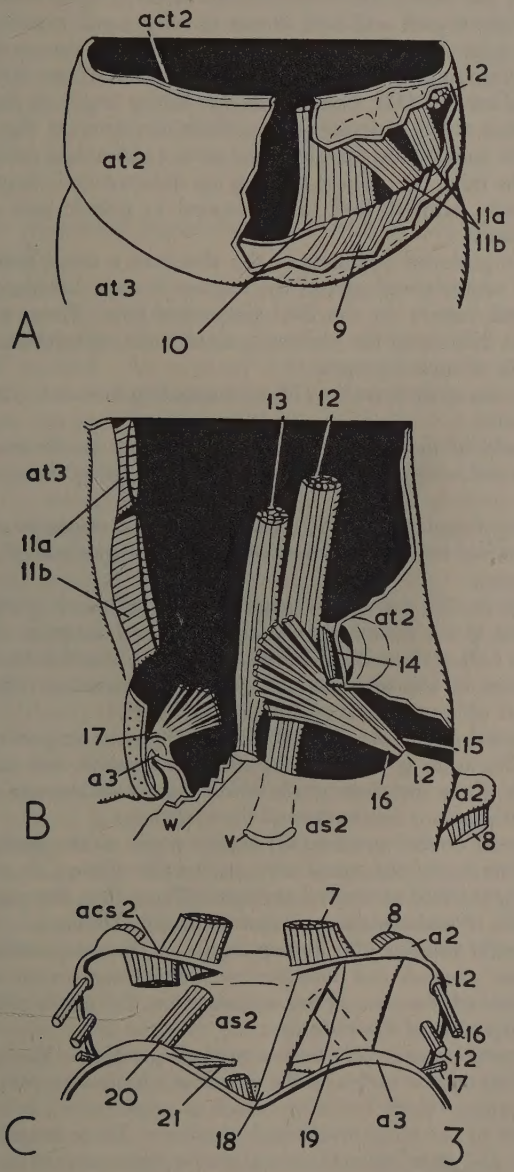

FIG. 3.—*Urocerus gigas gigas* (L.) female.

A. Dorsal view of dissection of second abdominal segment.
B. Lateral view of dissection of second abdominal segment.
C. Dorsal view of dissection, showing muscles of second abdominal sternum.

circular area on the second abdominal tergum which is more heavily sclerotised than the rest of the tergum and dark brown in colour, and insertion on a small crescentic ridge (*fig.* 3B, v) *on the dorsolateral edge of the second abdominal sternum.*—These muscles are dorsoventral compressors of the abdomen.

Tergo-sternal muscles (*13*), *smaller than 12, having origin on the second abdominal tergum close to but posterior to 12.*—Each inserts on *w* (fig. 3B), an oval projection on the dorsolateral margin of the second abdominal sternum posterior and dorsal to the ridge (*v*). These muscles are dorsoventral compressors of the abdomen. Muscle pairs 12 and 13 correspond to muscle pair 4 of the first abdominal segment.

On the more posterior segments of the abdomen a small group of muscles runs from each ventrolateral part of the tergum to each dorsolateral surface of the sternum and inserts on the oval projection (*w*). These muscles would appear to act as dilators of the abdomen, since their contraction separates the terga and sterna of each segment.

Occlusor muscles of the spiracles (*14*) *corresponding to muscle pair 5 of the first abdominal segment.*

Dilator muscles of the spiracles (*15*), *each inserting on the ventral arm of a spiracular valve and having origin on a lateral apodeme* (*l2*) *of the second abdominal sternum.*

A pair of fan-shaped muscles (*16*), *each of which has origin on a lateral part of the second abdominal tergum and insertion on a lateral apodeme* (*l2*) *of the second abdominal sternum.*

A similar but smaller pair of fan-shaped muscles (*17*), *each of which has origin on a lateral part of the second abdominal tergum and insertion on an anterior sternal apodeme* (*a3*) *of the third abdominal sternum.*—Muscles 16 and 17 are, in part, compressors of the abdomen, since their contraction lifts and swings forward the part of the sternum on which they insert.

Median internal ventral muscles (*18*) *having origin on the posterior part of the antecosta* (*fig.* 3C, acs2) *of the second abdominal sternum and insertion on the anterior surface of the antecosta of the third abdominal sternum.*—These thin, flat plates of muscles are contractors of the abdomen.

Lateral internal ventral muscles (*19*) *having origin on the posterior surface of the antecosta of the second abdominal sternum and insertion on the anterior surface of the antecosta of the third abdominal sternum.*—These thin, flat plates of muscles are broader than 18 and are also contractors of the abdomen.

External ventral muscles (*20*) *having origin on the anteromedian part of the second abdominal sternum and insertion on the anterior sternal apodemes* (a3) *of the third abdominal sternum.*—These are also thin, flat plates of muscles which function as contractors of the abdomen.

External ventral muscles (*21*) *with a reversed position.*—The origin of each of these muscles is narrow and is on the posterior and median part of the second abdominal sternum. Each insertion, which is more broad, is on an anterior sternal apodeme of the third abdominal sternum. These muscles function as extensors of the abdomen, since their contraction protracts the sterna by reducing the overlap between them.

IV. Apocrita

In this suborder the first abdominal segment forms anatomically a part of the thorax and is a propodeum. This word is sometimes used for the first

abdominal tergum only, but it should also include the sternum, which is usually present in a reduced form (Snodgrass, 1942 : 43). The terminology used for the abdominal segments of Apocrita differs in the different groups, and Richards (1956 : 39) is followed in using the term gaster for all the segments behind the propodeum and the term petiole for the narrow anterior stalk of the gaster, whether this stalk is composed of part of a segment or of one segment or of two.

A. *Parasitica*

The First Two Abdominal Segments of the Female of Rhyssa persuasoria *(L.). (Figs. 4, 5)*

The tergum of the propodeum forms a convex area, on the lateral edges of which are the prominent spiracles (*s1*). There are clear dorsal, ventral and lateral surfaces and the line of union between the propodeal tergum and the thorax is well marked. As in many Ichneumonidae, part of the surface is raised into keels, *i.e.* areolated (fig. 4C). A median depression is present anteriorly (fig. 4A) on the dorsal surface at the point of origin of some of the levator muscles of the abdomen (fig. 5B, *2*) and two further depressions are present on the posterior surface, each of them being more lateral than the anterior median depression. The lateral and posterior edges of the propodeum are raised into a thick ridge which strengthens the skeleton around the propodeal orifice (*see* fig. 4D). Above the part of the orifice where the gut, tracheal tubes, aorta and nerve cords leave the propodeum, there are two prominent skeletal projections, the propodeal teeth (*tr*), partly enclosing a region of the orifice which acts as a socket (*sr*) for the ridge (*r*) of the second abdominal tergum. This ridge, when viewed from the anterior end, is Y-shaped (fig. 4G, r), and the propodeal teeth fit into the ridge beneath each dorsal arm of the Y (*see* fig. 5A). As noted by Richards (1956), the second abdominal segment is articulated by its petiole to the propodeum by a double ball and socket joint. The ridge of the second abdominal tergum forms the ball of one of these joints and the remainder of the anterior end of the segment forms the ball of the other. The anterior edge of the tergum is folded to form a ridge, the lateral parts of which are larger than the median. These lateral parts may be called prephragmata (fig. 5A, *ph3*). The retractor muscles (not illustrated) of the mesothoracic postphragma arise on the anterior surfaces of the prephragmata and have anterolateral points of insertion on the mesophragma. The sternum (fig. 4B, D, *as1*) of the propodeum is a narrow ventral plate posterior to the hind legs.

The muscles of the first abdominal segment are as follows (fig. 5) :—

Levator muscles of the abdomen (2), *each having origin on the anterior, dorsal and lateral surfaces of the propodeal tergum and insertion by a broad and prominent tendon on the posterior edge of the ridge* (r) *of the second abdominal tergum* (fig. 5B). When the abdomen is lifted the anterior end of the abdomen pivots on the propodeal teeth, which are held in place by the ridge (*r*) of the second abdominal tergum. These levator muscles may be homologised with the median internal dorsal muscles of the first abdominal segment of Symphyta, this homology illustrating the condition summarised by Snodgrass in figure 1A, B.

Dorsolateral motor muscles of the abdomen (*3*), *each having origin on the dorsal and lateral surfaces of the propodeal tergum and insertion on each antero-*

lateral edge of the second abdominal tergum (*fig.* 5C).—These muscles, which may be homologised with the oblique internal lateral dorsal muscles of Symphyta, produce sidewise movements of the abdomen.

Occlusor muscles of the spiracles (*5*) *running between the arms of the spiracular valves, as in Symphyta.*

Dilator muscles of the spiracles (*6*) *which insert on the ventral arm of each spiracular valve and have origin on a small skeletal projection just dorsal to the socket of each hind leg.*

The sternum being reduced, the propodeum lacks ventral muscles and downwards movements of the gaster are brought about by the depressor muscles of the abdomen (*7*, *8*).—Each of these muscles consist of two groups. One has origin anteriorly on the transverse part of the endosternum of the metathorax (*e3*); the other has a more posterior origin on the median part of the metathoracic sternum. Both these groups of muscles insert by prominent tendons on the median part of the second abdominal sternum. As will be shown below, the median pair has a separate and more lateral position of insertion in other Apocrita.

Alam (1951, 1953) describes and figures two sets of levator muscles of the abdomen of *Stenobracon*. These both appear to correspond to the single pair of levator muscles of *Rhyssa*. Alam also describes and figures a pair of muscles arising on the metathoracic endosternum and inserting on the lateral edge of the second abdominal sternum. These muscles, which he calls meta-endosternal torsion muscles of the abdomen, appear to correspond to the ventral lateromotor muscles of the abdomen of other Apocrita—see muscle 8 in figures 7C, 9A, 11B They are, as already noted, absent in *Rhyssa*.

The second abdominal segment has a fairly short anterior petiole.

The tergum (fig. 4, *at2*) is somewhat flattened in form and its lateral edges bear marked grooves. The spiracles (*s2*) are dorsal to these grooves. The anterior end of the tergum bears the ridge (fig. 4E, F, G, *r*) on which the levator muscles of the propodeum insert. This ridge, which is covered by a dome of membrane (fig. 4A, C; fig. 5A, *e*), is Y-shaped when viewed from its anterior end and, as a whole, is pear-shaped when viewed dorsally, the wall of the ridge enclosing a central cavity (*see* fig. 4E).

The sternum (*as2*) consists of two skeletal plates, the posterior plate being lightly subdivided in the median line. The area of membrane between the tergum and sternum broadens markedly towards the posterior end of the segment.

The propodeum articulates with the second abdominal segment at three points—in the region of the propodeal teeth, in the region of the propodeal tergum and in the region of the first abdominal sternum. The second abdominal

---

FIG. 4.—*Rhyssa persuasoria* (L.) female.

A. Dorsal view of propodeum and second abdominal segment, which is shown with posterior end raised.

B. Ventral view of propodeum and second abdominal segment.

C. Lateral view of propodeum and second abdominal segment.

D. Posteroventral view of propodeum showing propodeal orifice and propodeal teeth.

E. Dorsal view of tergum of second abdominal segment showing dome of membrane (*e*) cut open to show ridge (*r*).

F. Lateral view of anterior end of second abdominal segment showing ridge.

G. Anterior view of second abdominal segment showing ridge.

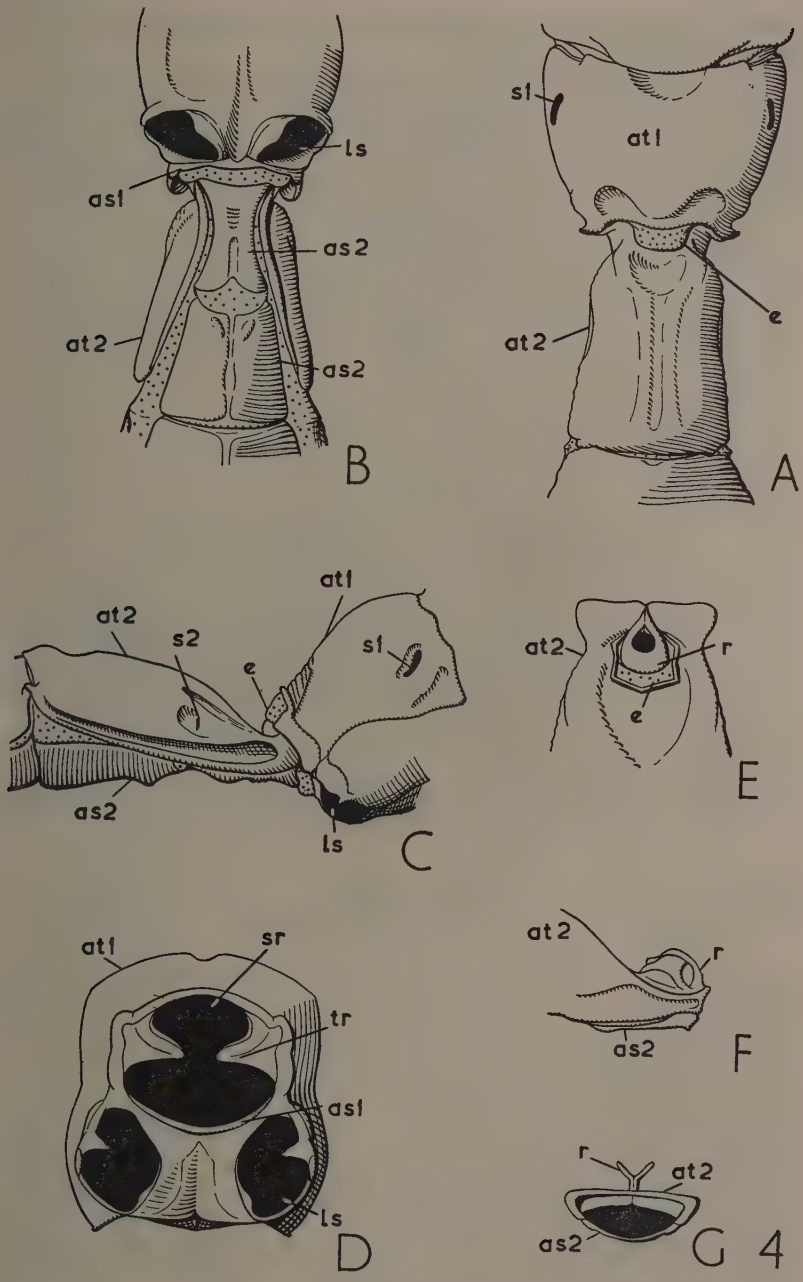

FIG. 4.—*Rhyssa persuasoria* (L.) female.

sternum fits into the propodeal orifice and rests on a ridge formed by the first abdominal sternum (fig. 5A, *as1*).

The muscles of the second abdominal segment are as follows (fig. 5B, C) :—

A large pair of median internal dorsal muscles (*10*) *having origin on the dorsal and lateral surfaces of the second abdominal tergum and insertion at median points on the antecosta of the third abdominal tergum* (at3).—These muscles may be homologised with the median internal dorsal muscles of the abdomen of Symphyta and they function as tergal retractors.

A small pair of tergo-sternal muscles (*12*), *each of which has a lateral and somewhat posterior origin on the second abdominal tergum and insertion on a posterior and lateral projection of the anterior plate of the second abdominal sternum* (as2).—These muscles, which are not shown by Alam in *Stenobracon*, may be homologised with the tergo-sternal muscles of the abdomen of Symphyta, and they function as dorsoventral compressors of the anterior part of the segment.

Occlusor muscles of the spiracles (*14*).

Dilator muscles of the spiracles (*15*), *each inserting on a ventral arm of the spiracular valve and having origin on the ventrolateral edge of the second abdominal tergum.*

Muscle fibres of the ventral diaphragm (not illustrated) insert on the postero-lateral projections of the anterior plate of the second abdominal sternum median to the point of insertion of the tergo-sternal muscles (12).

Internal ventral muscles (*18*, *19*), *thin and flat in form, having origin on the anterior edge of the posterior plate of the second abdominal sternum and on two lightly sclerotised areas in the membrane between the two plates of the sternum and insertion on the antecosta of the third abdominal sternum.*—These muscles, which may be homologised with the median and lateral internal ventral muscles of Symphyta, are contractors of the abdomen.

Alam describes and figures a pair of median and a pair of lateral internal ventral muscles in *Stenobracon*.

As will be seen below, the musculature of the second abdominal segment of *Rhyssa* is reduced in comparison with that of other Apocrita.

B. *Aculeata*

(*i*) *The First Two Abdominal Segments of the Queen of* Bombus lucorum (*L.*) (*Apoidea*). (Figs. 6, 7)

The tergum of the propodeum (*at1*) is more convex in form than that of *Rhyssa*. Both Duncan (1939) with *Vespula* and Snodgrass (1942) with the honey bee have pointed out that the thoracic segments and propodeum of these forms are condensed into a shape approaching that of a sphere, thus giving the body wall a form enabling it to withstand the stress put upon it by the powerful leg and wing muscles. Prominent spiracles (*s1*) are present on the lateral surfaces of the tergum and the line of fusion between the thorax and the tergum is distinct. The dorsal and lateral edges of the tergum around the propodeal orifice have a pronounced strengthening ridge. The propodeal teeth, which project into the propodeal orifice, are more dorsal in position than in *Rhyssa*, and almost meet in the median line to enclose a relatively small oval socket for the ridge of the second abdominal tergum. In *Bombus* the mesothoracic postphragma (fig. 6D, *2ph*) projects backwards and fills the cavity of the pro-

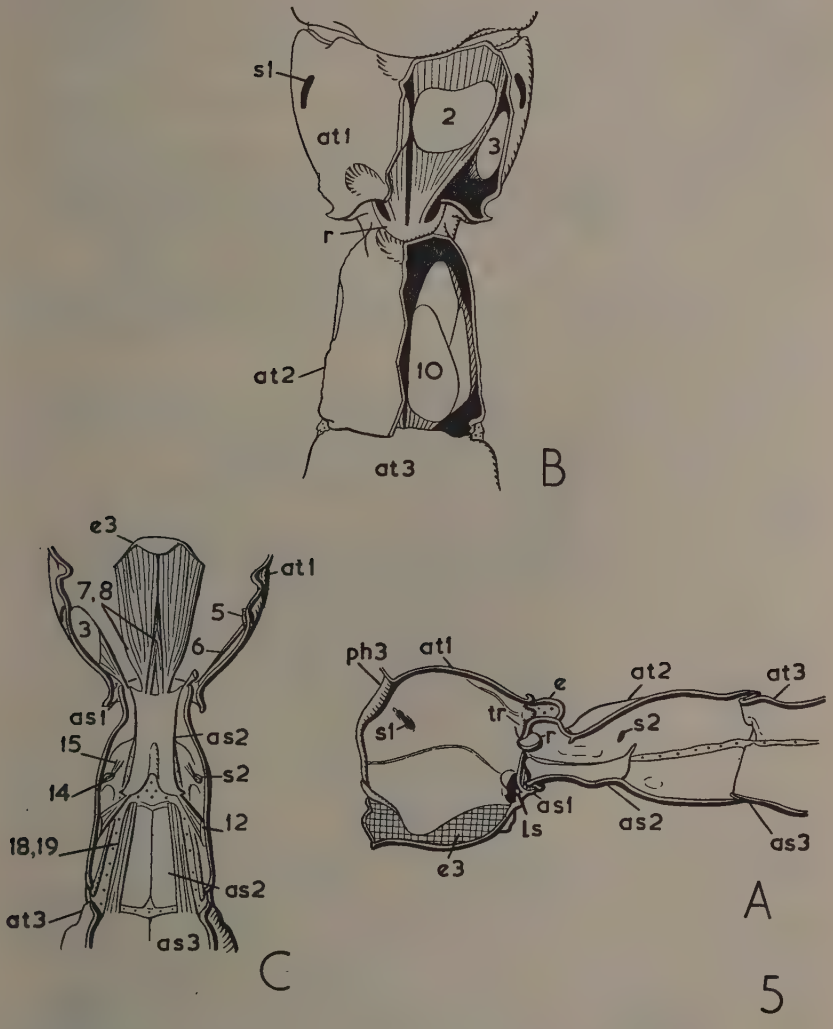

FIG. 5.—*Rhyssa persuasoria* (L.) female.

A. Lateral view of median longitudinal section of skeleton of propodeum and second abdominal segment, showing base of propodeal tooth (*tr*), with tip hidden by ridge (*r*).

B. Dorsal view of dissection of propodeum and second abdominal segment showing dorsal muscles.

C. Dorsal view of dissection of propodeum and second abdominal segment showing ventral and spiracular muscles.

podeum to a much more marked extent than in *Rhyssa*, so that the muscles of the propodeal tergum have a more lateral position than in *Rhyssa*. The greater degree of development of the dorsal wing muscles and mesothoracic postphragma in *Bombus* as compared with *Rhyssa* is presumably correlated with greater powers of flight.

The sternum of the propodeum (*as1*) is a narrow, ventral plate, V-shaped in form and situated posterior to the hind legs (*ls*).

In the following description of the muscles they will be compared with those of the honey-bee, of which an admirable account has been given by Snodgrass (1942, 1956), with those of *Rhyssa*, and, in the case of the muscles of the second abdominal segment, with those of *Urocerus*. References to earlier studies on the honey-bee will be found in Snodgrass's accounts.

The muscles of the propodeal tergum are as follows (fig. 6D, 7A) :—

Levator muscles of the abdomen (*2*), *similar to the levator muscles of* Rhyssa, *but with entirely lateral points of origin.*—These muscles are very similar in form and position to those of the honey-bee.

Dorsolateral motor muscles of the abdomen (*3*), *much more slender than the corresponding muscles in* Rhyssa, *and each having an entirely lateral origin ventral and just anterior to the spiracle.*—In the honey-bee each muscle has origin in two branches, one dorsal and one ventral to the spiracle.

The occlusor (*5*) *and dilator* (*6*) *muscles of the spiracles, similar in form and position to those of* Rhyssa *and the honey-bee.*

The propodeal sternum is reduced and the ventral muscles of the abdomen have origin on the fused endosterna of the meso- and metathorax (*e2*, *3*) and on the metathoracic sternum.

The median depressors of the abdomen (*fig.* 7C, 7), *triangular in form and each with a broad origin on the transverse part of the endosterna and insertion by a prominent tendon on the median part of the antecosta* (acs2) *of the second abdominal sternum* (as2).—Similar muscles, each triangular in shape, but with a much more narrow origin, are present in *Rhyssa* and in the honey-bee.

The ventral lateromotor muscles of the abdomen (*8*), *more slender in form and having origin on the metathoracic sternum and insertion on each lateral edge of the antecosta of the second abdominal segment.*—These muscles have a similar form and position in the honey-bee, but in *Rhyssa* their point of insertion is median to the median depressors and their function therefore differs.

In *Bombus* and in the honey-bee, probably as a result of the posterior projection of the mesothoracic postphragma (fig. 6D, *2ph*), the retractor muscles of the postphragma (23) arise on a median and posterior projection of the propodeal tergum and not on the propodeal prephragmata as in *Rhyssa*.

The second abdominal tergum is narrow in the antero-posterior direction and broad in a transverse direction. The petiole is short and the median and anterior surface of the tergum (fig. 6B, *at2*) is concave so as to enclose the

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FIG. 6.—*Bombus lucorum* (L.) queen.

A. Lateral view of propodeum and second abdominal segment.
B. Dorsal view of propodeum and second abdominal segment with the latter depressed.
C. Posterior view of anterior end of skeleton of second abdominal segment.
D. Dorsal view of dissection of propodeum and second abdominal segment.

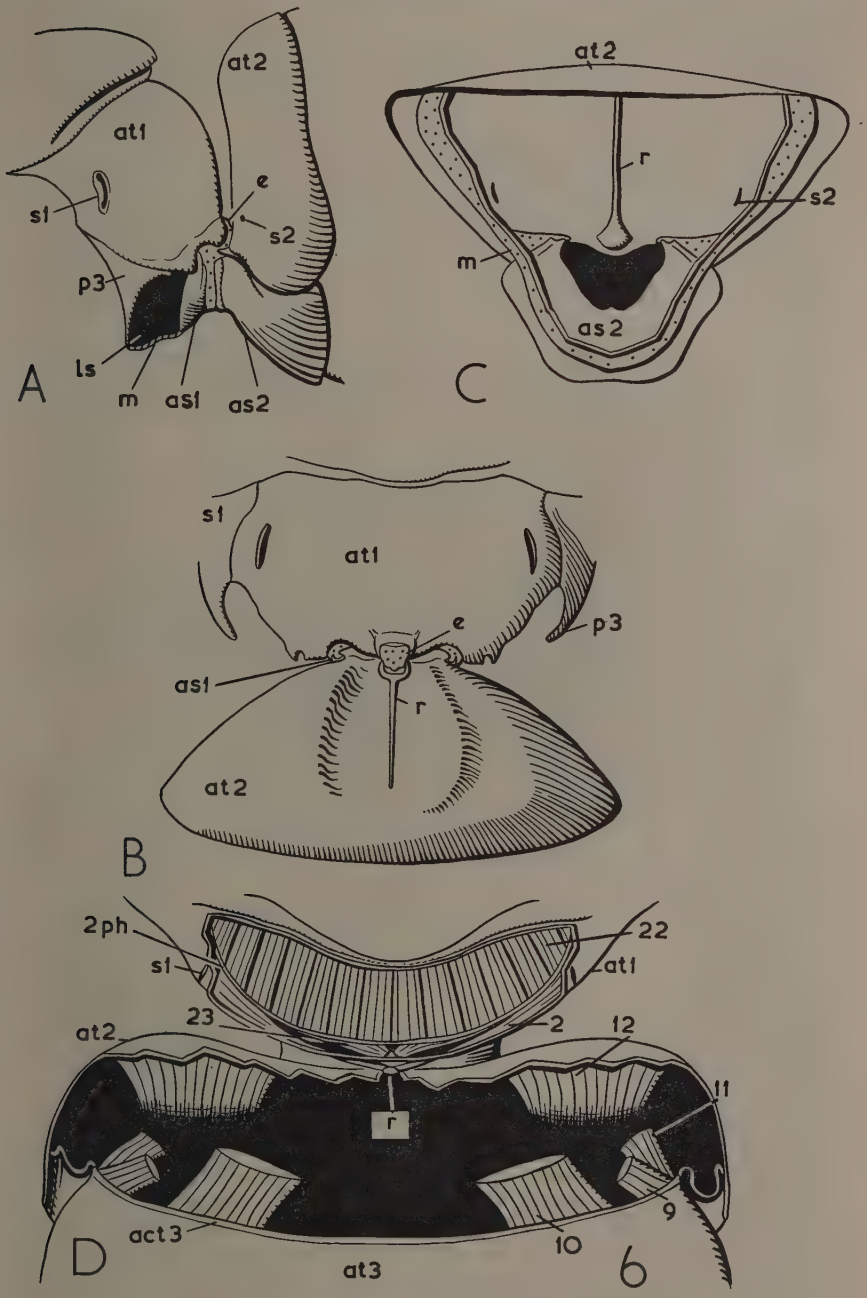

FIG. 6.—*Bombus lucorum* (L.) queen.

posterior part of the propodeal tergum when the abdomen is lifted. A ridge (*r*) runs along the median line of this concavity and ends in a structure for the insertion of the levator muscles of the abdomen and for articulation with the propodeal teeth similar to, but relatively smaller than, that of *Rhyssa*. This end part of the ridge is enclosed in a dome of membrane (*e*).

Small spiracles (*s2*) are present on the anterolateral surfaces of the tergum

The sternum (*as2*), the lateral parts of which are overlapped by the tergum, is also narrow in the anteroposterior direction, but is less broad than the tergum in a transverse direction (fig. 6C). There is a well developed antecosta (fig. 7C, *acs2*).

The muscles of the second abdominal segment are as follows (figs. 6D, 7B, C) :—

External dorsal muscles (*9*), *each having origin on the dorsal and posterior part of the second abdominal tergum and insertion on a lateral part of the antecosta* (act3) *of the third abdominal tergum* (at3).—These muscles are extensors of the abdomen. Similar muscles are present in the honey-bee and in *Urocerus*, but they are absent in *Rhyssa*.

Median internal dorsal muscles (*10*), *each having origin on the median dorsal part of the second abdominal tergum and a more lateral insertion on the antecosta of the third abdominal tergum*.—These muscles are tergal retractors. Similar muscles are present in the honey-bee, *Urocerus* and *Rhyssa*.

Oblique lateral dorsal muscles (*11*), *each having a dorsal and somewhat lateral origin on the second abdominal tergum and insertion on a lateral edge on the antecosta of the third abdominal tergum*.—These muscles are also tergal retractors. Similar muscles exist in the honey-bee and in *Urocerus*, where each muscle consists of two parts. They are absent from *Rhyssa*.

Tergo-sternal muscles (*12*) *having origin on the anterodorsal part of the tergum and insertion on the lateral parts of the second abdominal sternum* (*fig.* 7C, as2).—These muscles are dorsoventral compressors of the abdomen. Similar muscles are present in the honey-bee, *Urocerus* and *Rhyssa*. In the more posterior segments there are three lateral tergo-sternal muscles to each segment, as in the honey-bee. In *Urocerus* there is one pair of tergo-sternal muscles in the first abdominal segment but two in the second.

Occlusor muscles of the spiracles (*fig.* 7B, *14*), *running between the arms of the spiracular valves*.—Similar muscles are present in the honey-bee, *Urocerus* and *Rhyssa*.

Dilator muscles of the spiracles (*15*), *each inserting on the ventral arm of a spiracular valve and having origin on an anterolateral edge of the second abdominal sternum*.—Similar muscles are present in the honey-bee and in *Urocerus*. In *Rhyssa* these muscles have origin on the second abdominal tergum.

Internal ventral muscles (*18, 19*), *having origin on the posterior surface of the antecosta* (acs2) *of the second abdominal sternum and a more median insertion on the anterior surface of the antecosta of the third abdominal sternum*.—These muscles are contractors of the abdomen. Similar muscles are present in the honey-bee, in *Urocerus*, where each muscle consists of two distinct parts, and in *Rhyssa*.

External ventral muscles (*20*), *each having origin on the anteromedian part of the second abdominal sternum and insertion on a part of the third abdominal sternum representing the anterior and lateral apodemes* (a3, l3) *of the honey-bee and* Urocerus *fused*.—These muscles function as contractors of the abdomen.

Similar muscles are present in the honey-bee and in *Urocerus*. They are absent from *Rhyssa*.

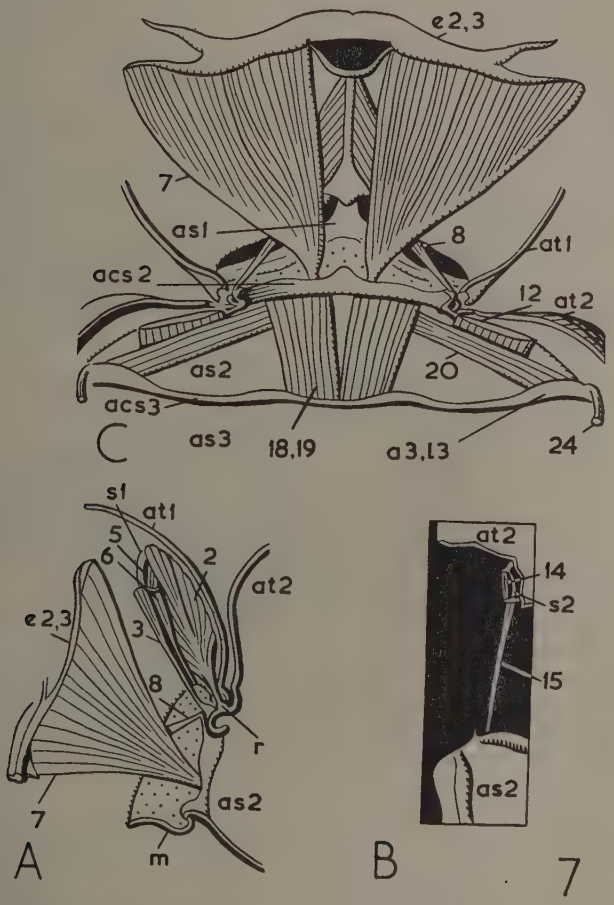

FIG. 7.—*Bombus lucorum* (L.) queen.

A. Dorsolateral view of dissection of propodeum to show muscles. Sternum of the propodeum not shown.

B. Lateral view of dissection of second abdominal segment to show spiracular muscles.

C. Dorsal view of dissection showing depressor and ventral lateromotor muscles of abdomen and ventral muscles of second abdominal segment.

Reversed external ventral muscles are absent from *Bombus*, but they are present in the honey-bee and in *Urocerus*.

A small reversed muscle (24) having origin on each anterolateral edge of the third abdominal tergum and insertion dorsally on each fused anterior and lateral apodeme of the third abdominal sternum.—These muscles are dilators of the abdomen.

It will be seen that, although there is some reduction of the musculature of the second abdominal segment of *Bombus* and the honey-bee in comparison with that of *Urocerus*, this still retains a relatively unspecialised pattern. In *Rhyssa*, on the other hand, there is a very obvious reduction and specialisation of the musculature of this segment. The depressor and lateromotor muscles of the abdomen of *Rhyssa* are also specialised in comparison with those of bees.

(*ii*) *The First Two Abdominal Segments of the Queen of* Vespula vulgaris (*L.*) (*Vespoidea*). (*Figs. 8, 9*)

The tergum of the propodeum (*at1*) is generally convex in form, although the anterodorsal surface is emarginated and posterior to this emargination there is a shallow depression. Deep grooves, marking internal strengthening ridges, run on each posterolateral surface of the tergum, and a pattern of grooves is present on the posteromedian surface. Relatively large propodeal teeth (*tr*) project into the propodeal orifice. Prominent spiracles (*s1*) are present on the anterolateral surfaces of the tergum. The line of fusion between the tergum and the thorax is clear only in its dorsal and dorsolateral parts.

The sternum of the propodeum (*as1*) is reduced to a narrow plate beneath the propodeal orifice and behind the hind legs.

In the account of the muscles they will be compared with those of the thorax of *Vespa crabro* L. described by Weber (1925) and, where relevant, with those of other Hymenoptera examined for the present account. An excellent description of the skeleto-muscular system of the queen of *Vespula pensylvanica* (Sauss.) has been given by Duncan (1939), and the species studied in the present account was found to agree very closely with this description.

The muscles of the propodeal tergum are as follows (fig. 9A):—

Levator muscles of the abdomen (*2*), *similar in form and position to those of bees and* Vespa.

Dorsolateral motor muscles of the abdomen (*3*), *each having origin on the lateral surface of the tergum dorsal to the spiracle.*—These are much larger muscles than those of bees. Similar muscles exist in *Vespa.*

The occlusor (*5*) *and dilator* (*6*) *muscles of the spiracles, similar in form and position to those of bees and* Vespa.

The ventral muscles of the abdomen are as follows :—

The median depressors of the abdomen (7), *generally similar in form and position to those of bees.*—In *V. vulgaris* each muscle consists of two parts, one having origin on the transverse part of the metathoracic endosternum (*e3*) and the other, a slender lateral strand, having origin on the metapleural apodeme. In *V. pensylvanica* this separation of the muscle parts appears to be more distinct. Duncan considers these parts to be two distinct muscles, but it is doubtful whether this interpretation is necessary. Weber appears to figure these muscles in *Vespa*, but he describes them as leg muscles and his diagrams and account are confused.

The ventral lateromotor muscles of the abdomen (8), *generally similar in form and position to those of bees, but each consisting of two parts.*—In *V. pensylvanica* and in *Vespa* each muscle consists of only one group of fibres.

In *Vespula* and *Vespa* the retractor muscles of the mesopostphragma are better developed than in *Rhyssa* and arise on the anterior surfaces of the propodeal prephragmata (fig. 9A, *ph3*). Each inserts anteriorly and laterally on

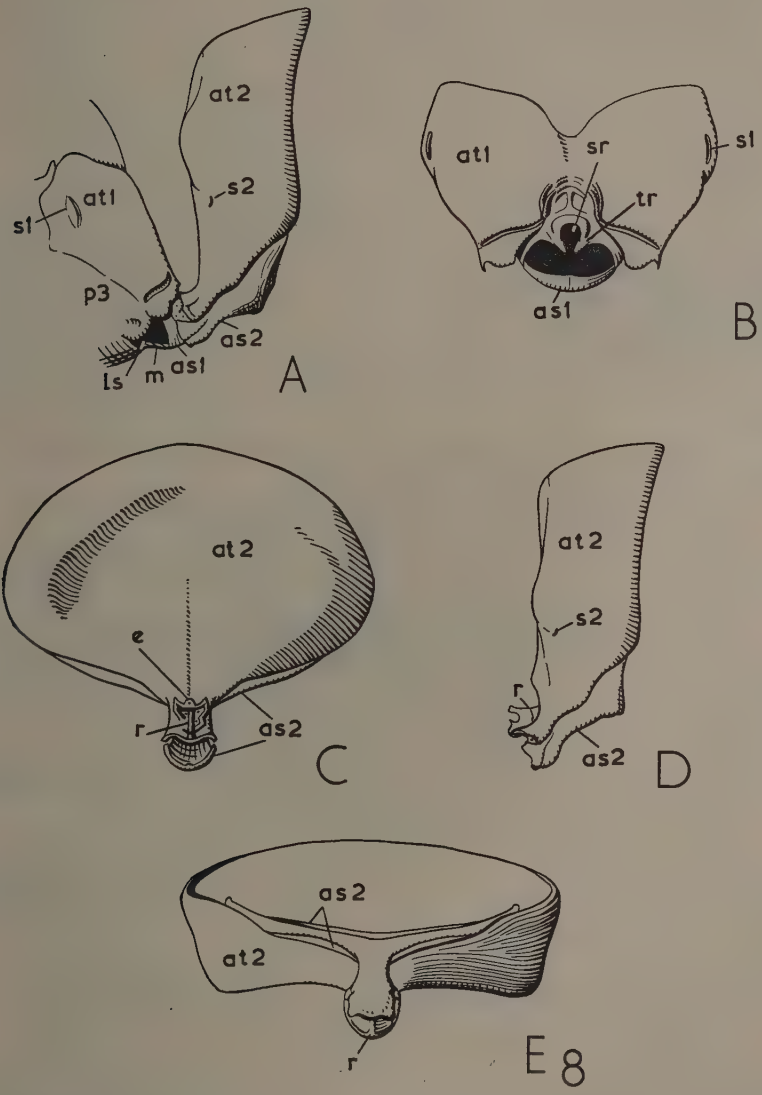

FIG. 8.—*Vespula vulgaris* (L.) queen.

A. Lateral view of propodeum and second abdominal segment.
B. Posteroventral view of the propodeum showing propodeal orifice.
C. Anterodorsal view of second abdominal segment.
D. Lateral view of second abdominal segment.
E. Ventral view of second abdominal segment.

the postphragma. In bees these retractor muscles have origin on a median and posterior projection of the propodeal tergum.

The second abdominal tergum (*at2*), like that of *Bombus*, is narrow in the anteroposterior direction and broad in a transverse direction. The petiole is short and the median and anterior surface of the tergum (fig. 8C) is, like that of *Bombus*, concave so as to enclose the posterior part of the propodeal tergum when the abdomen is lifted. The structures for articulation with the propodeal teeth (fig. 8C, D) are similar to those of *Bombus*.

Small spiracles (*s2*) are present on the lateral surfaces of the tergum.

The sternum (*as2*), the lateral edges of which are overlapped by the tergum, is reduced to a narrow Y-shaped strip, with the stem of the Y anterior in position. The tergum and sternum are fused at the anterior end of the segment, but not at the posterior end. There is a well developed antecosta and the lateral edges of the sternum have prominent ridges (fig. 9C, *rg2*) which presumably represent, in part, the anterior and lateral apodemes fused.

The muscles of the second abdominal segment are as follows (fig. 9B, C) :—

Median internal dorsal muscles (*10*), *similar in form and function to those of bees.*

Oblique lateral dorsal muscles (*11*), *generally similar in form and function to those of bees but each having two distinct branches.*

Tergo-sternal muscles (*12*), *similar in form and function to those of bees.*

Occlusor muscles of the spiracles (*14*), *similar to those of bees.*

Dilator muscles of the spiracles (*15*), *each inserting on the ventral arm of a spiracular valve and having origin on the posterior part of the ridge* (rg2) *which corresponds to the fused apodemes.*

Ventral muscles of the second abdominal segment, greatly reduced, there being present only reversed external ventral muscles (*21*), *each having origin on a median and lateral part of the sternum and insertion on a fused anterior and lateral apodeme* (*a3*, *l3*) *of the third abdominal sternum* (as3).—These muscles, although absent in this segment in *Bombus*, are present in the honey-bee.

The sternal muscles of the third abdominal segment are more generalised and there are present, as well as *reversed external muscles* (*27*), *internal and external ventral muscles* (*25 and 26*) *similar to those of bees.*

Wheeler (1928) derives the social Vespoids and Formicoids from primitive Vespoids and it is probable that this specialisation of the second abdominal segment of wasps is a condition foreshadowing that of ants, where the petiole consists of one or two segments.

(*iii*) *The First Three Abdominal Segments of the Male of* Dorylus (*subgenus* Alaopone) *sp.* (*Formicoidea*). (*Figs. 10, 11*)

The tergum of the propodeum (*at1*) is less round in form than that of *Bombus* and *Vespula*, the dorsal and lateral surfaces being flat and the posterior surface, which is also flat, meets the dorsal and lateral surfaces at a sharp angle. Relatively large propodeal teeth (fig. 11E, *tr*) project into the propodeal orifice to mark off an oval socket (*sr*) for the ridge of the second abdominal tergum. Prominent spiracles (fig. 10, *s1*) project from the lateral surfaces of the tergum. The line of fusion between the tergum and the thorax is clearly visible. The mesothoracic postphragma does not project into the cavity of the propodeum to the same extent as in *Bombus*, and, as in *Vespula*, the retractor muscles arise

on the prephragmata of the propodeum, although these are much more poorly developed than those of *Vespula*. Although the male of *Dorylus* is a strong flier (Skaife, 1954), the wings appear to be used only once in the life cycle.

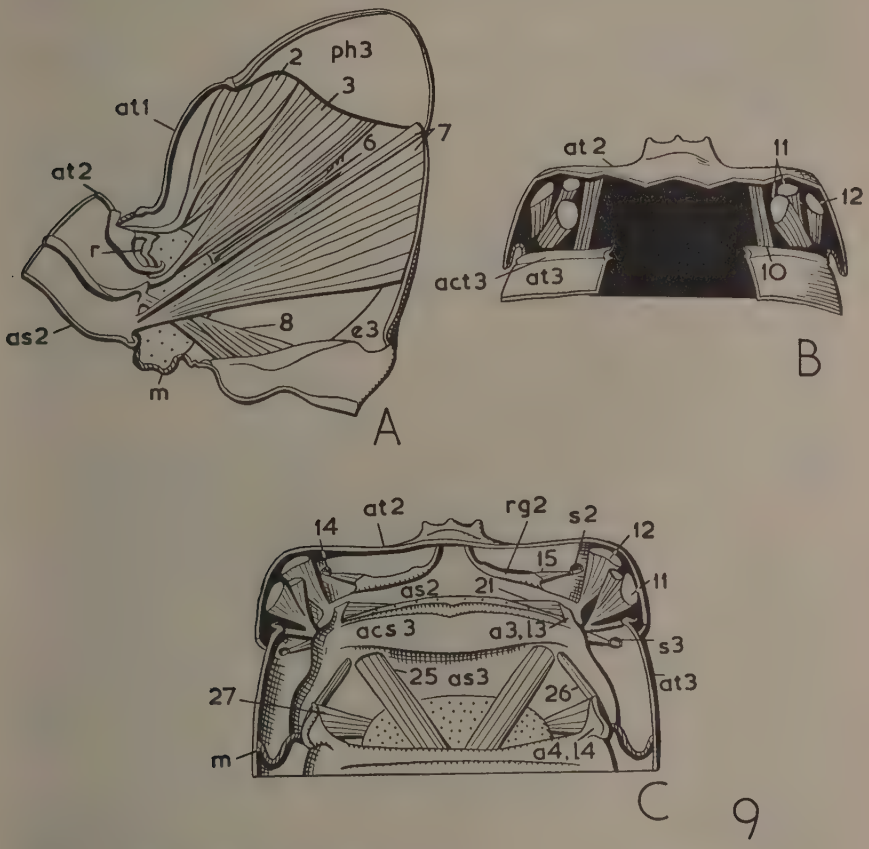

FIG. 9.—*Vespula vulgaris* (L.) queen.

A. Lateral view of dissection showing spiracular muscles of propodeum and levator, depressor and lateromotor muscles of abdomen.

B. Dorsal view of dissection of second abdominal segment to show dorsal muscles.

C. Dorsal view of dissection of second and third abdominal segments to show ventral muscles.

The sternum (*as1*) of the propodeum is a narrow ventral plate posterior to the hind legs.

In the following description of the muscles they will be compared principally with those of *Vespula*, with those of *Lasius* as described by Lubbock (1879), and with those of *Myrmica* as described by Janet (1894, 1897). The muscles of the propodeal tergum are as follows (fig. 11A):—

Levator muscles of the abdomen (*2*), *generally similar to those of* Vespula, *but each having a more dorsal origin.*

Dorsolateral motor muscles of the abdomen (*3*), *generally similar to those of* Vespula, *but each having a more dorsal origin.*—The position of these two pairs of dorsal muscles is probably correlated with the size and position of the meso-thoracic postphragma.

Occlusor (*5*) *and dilator* (*6*) *muscles of the spiracles, similar in form and position to those of* Vespula.

The ventral muscles of the abdomen are as follows (fig. 11B) :—

Median depressors of the abdomen (*7a*), *each of which is a large muscle having a broad origin on the transverse part of the metathoracic endosternum* (e3) *and a more narrow insertion on the antecosta of the second abdominal sternum* (as2).

Accessory lateromotor muscles of the abdomen (*7b*), *each of which is a slender strand arising on the transverse part of the metathoracic endosternum lateral to each median depressor and inserting on the lateral edge of the sternum of the second abdominal segment.*—These muscles were present in two specimens dissected but not in another. They are so slender that their contraction can have little effect on the abdomen.

Ventral lateromotor muscles of the abdomen (*8*), *similar in form and function to those of* Vespula.

The motor muscles of the abdomen of *Lasius* and *Myrmica* are generally similar to those of *Dorylus*, although the accessory lateromotor muscles are absent.

The entire second abdominal segment is considered to form the petiole. The anterior end forms a narrow projection (fig. 11F) which fits into the propodeal orifice, and the posterior end is inturned to form a rim enclosing the narrow anterior end of the third abdominal segment.

The tergum (*at2*) is oblong in shape when viewed dorsally and there are definite dorsal and lateral surfaces. Small spiracles (*s2*) are situated on the anterolateral surfaces. On the mid-dorsal part of the anterior projection of the tergum there is a ridge of the usual form (figs. 10D, 11F, *r*) which fits into the dorsal part of the propodeal orifice (fig. 11E, *sr*) and articulates with the propodeal teeth (*tr*).

The sternum (fig. 10, *as2*) is smaller than the tergum and, when viewed from the ventral surface, can be seen to be raised into a steep, keel-like ridge. The tergum and sternum, like those of *Vespula*, are fused at the anterior end of the segment. At the line of fusion the edges of the tergum and sternum are raised into ridges (fig. 10D, 11D, *rg2*), those of the sternum being larger than those of the tergum.

The muscles of the second abdominal segment are as follows (fig. 11C, D) :—

Median internal dorsal muscles (*10*), *similar in form and function to those of* Vespula, Lasius *and* Myrmica.

Oblique lateral dorsal muscles (*11*), *each having origin on the dorsal and antero-lateral surfaces of the tergum and insertion on the antecosta of the sternum of the third abdominal sternum* (as3).—The points of insertion of homologous muscles in *Bombus* and *Vespula* are on the ventrolateral edges of the tergum of the third abdominal segment and the points of insertion in *Dorylus* have shifted slightly to be clearly sternal. The muscles are powerful and function as depressors of the abdomen, in contrast to the homologous muscles in *Bombus* and *Vespula*,

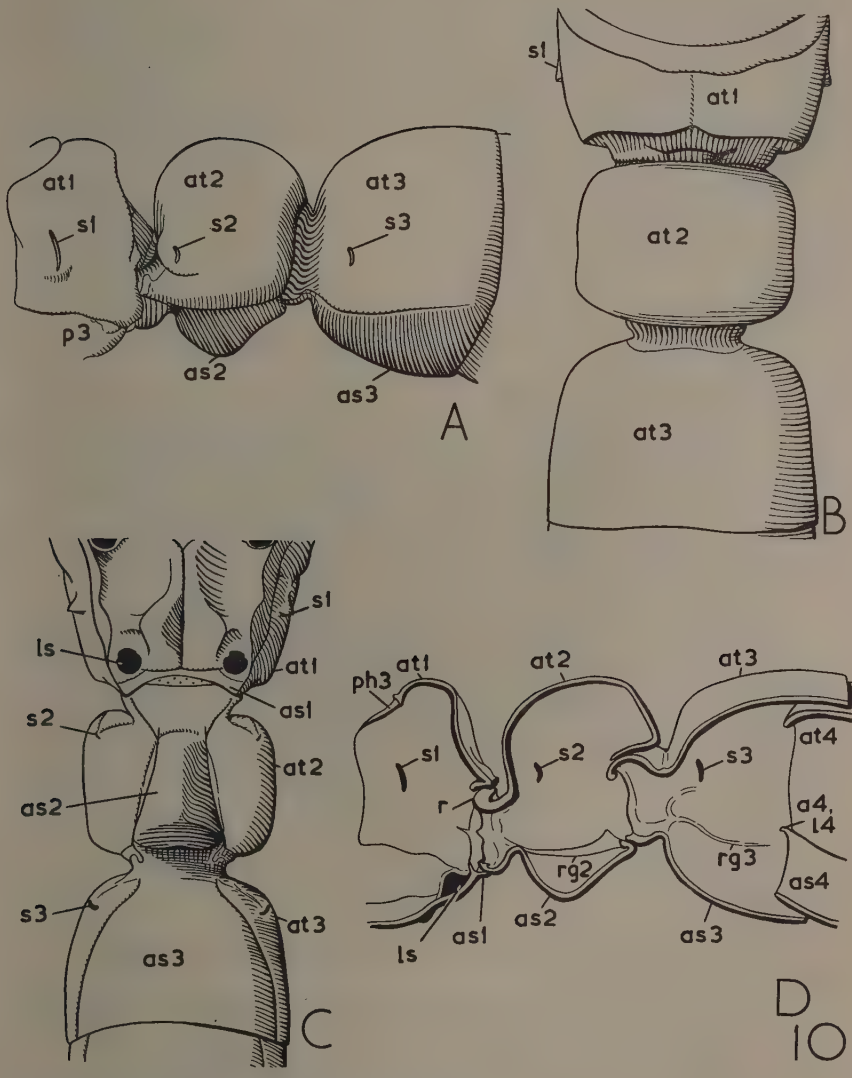

FIG. 10.—*Dorylus* (subgenus *Alaopone*) *sp.* male.

A. Lateral view of propodeum and second and third abdominal segments.
B. Dorsal view of propodeum and second and third abdominal segments.
C. Ventral view of propodeum and second and third abdominal segments.
D. Lateral view of median longitudinal section of skeleton of propodeum and second and third abdominal segments with membrane between segments omitted.

which are tergal retractors. The petiole of ants consists of one or two segments. In *Dorylus*, although the petiole is considered to consist of one segment, the anterior end of the third abdominal segment is narrow to ensure a high degree of mobility. The alteration in form and function of the oblique lateral dorsal muscles is associated with this skeletal specialisation. These muscles have a similar position in *Lasius*. Janet describes muscles corresponding to the oblique lateral dorsal and external dorsal muscles inserting on the tergum of the third abdominal segment of *Myrmica*.

Tergo-sternal muscles (*12*), *each having origin on a dorsolateral and posterior part of the tergum and insertion on each lateral edge of the inturned rim of the posterior end of the second abdominal sternum*.—These muscles function as dorso-ventral compressors of the abdomen and are generally similar in form and function to those of *Vespula*. They are absent from the second abdominal segment of *Lasius* and *Myrmica*.

Occlusor muscles of the spiracles (*14*), *similar in form and function to those of* Vespula *and* Myrmica.

Dilator muscles of the spiracles (*15*), *each inserting on the ventral arm of a spiracular valve and having origin on the anteroventral edge of the tergum*.—This appears to be a specialised condition since, although these muscles also have origin on the tergum in the third abdominal segment, they have origin on the sternal apophyses in the fourth segment. They also have origin on the sternal apophyses in the more posterior segments of *Myrmica*.

Sternal skeletal muscles are absent from the second abdominal segment of *Dorylus*, *Lasius* and *Myrmica*.

The third abdominal segment is modified at the anterior end, where it forms a projection which fits into and articulates with the inturned posterior part of the second segment. The posterior end of the segment is not modified and overlaps the anterior end of the fourth abdominal segment. The tergum (*at3*) has small spiracles (*s3*) on its lateral surface, the sternum (*as3*) is much broader than that of the second segment and the tergum and sternum are fused along their entire lengths. The third abdominal segment is therefore considerably modified as compared with the fourth.

The muscles of the third abdominal segment are as follows (figs. 11c, D):—

External dorsal muscles (*30*) *functioning as extensors of the abdomen.*

Median internal dorsal muscles (*28*) *functioning as tergal retractors.*

Oblique lateral dorsal muscles (*29*) *functioning as tergal retractors.*

Occlusor and dilator muscles of the spiracles (s3).

Internal ventral muscles (*25*) *and external ventral muscles* (*26*) *functioning as contractors of the abdomen.*

Reversed external ventral muscles (*27*) *functioning as extensors of the abdomen.*

Fig. 11.—*Dorylus* (subgenus *Alaopone*) *sp.* male.

A. Dorsal view of dissection of propodeum showing muscles.

B. Dorsal view of dissection showing spiracular muscles of propodeum and depressor and ventral lateromotor muscles of abdomen.

C. Dorsal view of dissection of second and third abdominal segments showing dorsal muscles.

D. Dorsal view of dissection of second and third abdominal segments showing ventral muscles.

E. Posterior and slightly ventral view of propodeum.

F. Dorsal and slightly anterior view of anterior end of second abdominal segment.

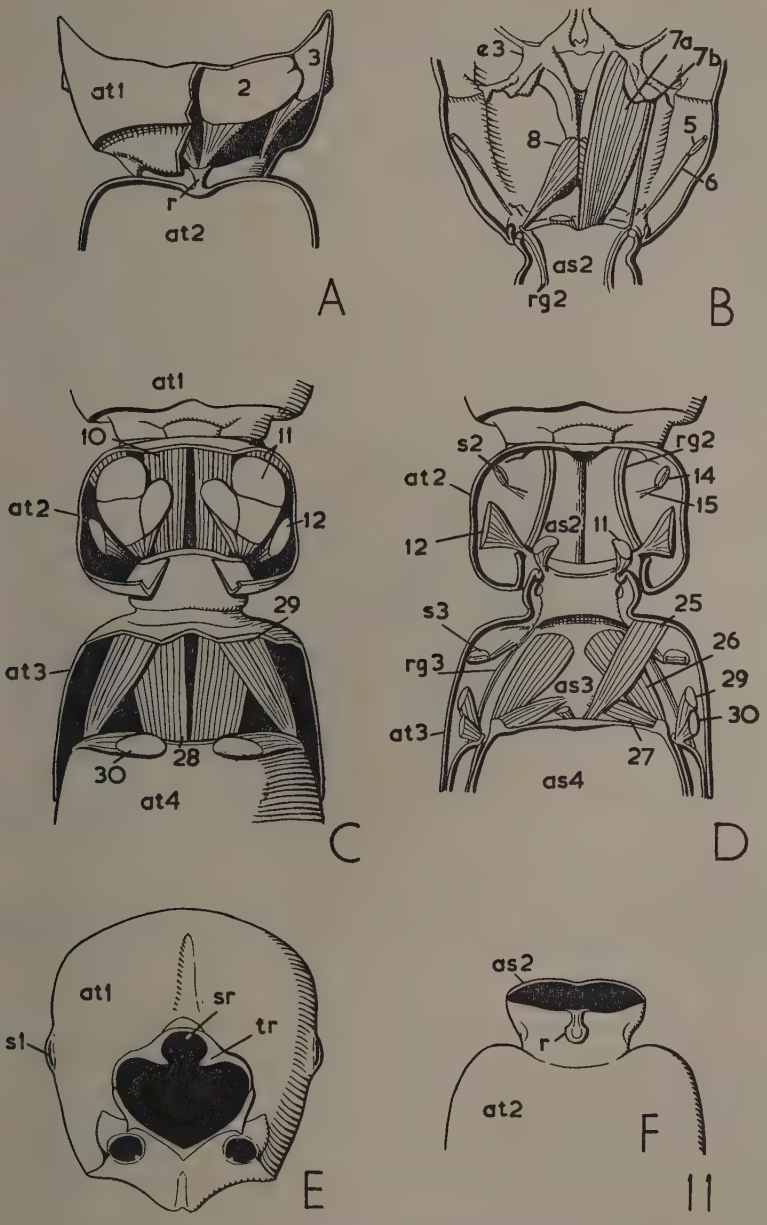

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FIG. 11.—*Dorylus* (subgenus *Alaopone*) *sp.* male.

It will be seen that, apart from the absence of tergo-sternal muscles which is probably associated with the fusion of tergum and sternum, the musculature of the third abdominal segment has a generalised pattern. The musculature of this segment is generally similar in *Myrmica*, where tergo-sternal muscles are present.

The modification of the second and third abdominal segments of *Dorylus* as compared with other Apocrita may be connected with a different system of mobility in the abdomen. The author has observed movements of raising and lowering the gaster and an almost semicircular curving of the segments of the gaster behind the petiole in various ichneumonoids when ovipositing. Similar movements have been observed in a wasp and in a honey-bee stinging. However a wood ant worker, when squirting formic acid, was observed to swing the gaster forward beneath the thorax so that the posterior end was pointing in the same direction as the head. It will be recalled that, in *Dorylus* at least, there are powerful depressor muscles of the abdomen (fig. 11c, 11) capable of bringing about such a movement.

V. Summary

The skeleto-muscular mechanisms of the anterior abdominal segments have been examined in the adults of *Urocerus*, *Rhyssa*, *Bombus*, *Vespula* and *Dorylus*.

In *Urocerus* the skeleto-muscular system is similar to that of most winged insects. Dorsal motor muscles between the thorax and abdomen are absent and ventral muscles are poorly developed.

In the Apocrita the dorsal and ventral muscles of the first abdominal segment (which is fused with the metathorax) form dorsal and ventral motor muscles of the gaster. Little is certain about the phylogeny of the Apocrita and it is not possible to outline a trend in evolution for the petiole region. The musculature of the propodeum and the skeletal parts for articulation between the petiole and propodeum are basically similar in all Apocrita.

The second abdominal segment retains the most complete pattern of musculature in bees. This musculature is reduced in *Rhyssa* and *Vespula*, although in different ways. The condition in *Vespula* foreshadows that of *Dorylus*, where ventral muscles are absent.

The type of abdominal mobility in *Dorylus* appears to differ from that of other Apocrita and certain dorsal muscles of the second abdominal segment are modified to form depressors of the abdomen.

VI. List of Muscles

1. Reversed external dorsal muscles of the first abdominal segment of *Urocerus* which function as extensors of the abdomen.

2. Median internal dorsal muscles of the first abdominal segment, functioning as tergal retractors in *Urocerus* and as levators of the abdomen in Apocrita.

3. Oblique internal lateral dorsal muscles of the first abdominal segment, functioning as tergal retractors in *Urocerus* and producing sidewise movements of the abdomen in Apocrita.

4. Tergo-sternal muscles of the first abdominal segment of *Urocerus* which function as dorsoventral compressors of the abdomen.

5. Occlusor muscles of the spiracles of the first abdominal segment.

6. Dilator muscles of the spiracles of the first abdominal segment.

7. Internal ventral muscles functioning as sternal retractors of the abdomen in *Urocerus* and depressors of the abdomen in Apocrita.

8. Lateral internal ventral muscles. These are specialised in *Urocerus*, where each runs between the anterior sternal apodemes of the second abdominal segment and the coxae of the hind legs. In most Apocrita these muscles function as ventral lateromotors of the abdomen and have origin on the metathoracic sternum and insertion on each lateral edge of the antecosta of the second abdominal sternum. The position and function of these muscles are modified in *Rhyssa*.

9. Reversed external dorsal muscles of the second abdominal segment which function as extensors of the abdomen. These muscles are present in *Urocerus* and bees, but absent in *Rhyssa*, *Vespula* and *Dorylus*.

10. Median internal dorsal muscles of the second abdominal segment which function as tergal retractors.

11. Oblique lateral dorsal muscles of the second abdominal segment which function as tergal retractors. They are absent in *Rhyssa*, but present in other Apocrita and in *Urocerus*. In *Dorylus* these muscles are modified to act as depressors of the abdomen.

12. Tergo-sternal muscles of the second abdominal segment which function as dorsoventral compressors of the abdomen.

13. Tergo-sternal muscles of the second abdominal segment of *Urocerus* which function as dorsoventral compressors of the abdomen.

14. Occlusor muscles of the spiracles of the second abdominal segment.

15. Dilator muscles of the spiracles of the second abdominal segment.

16, 17. Small fan-like groups of muscles of the second abdominal segment of *Urocerus* which function as compressors of the abdomen.

18. Median internal ventral muscles of the second abdominal segment of *Urocerus* functioning as contractors of the abdomen.

19. Lateral internal ventral muscles of the second abdominal segment of *Urocerus* functioning as contractors of the abdomen.

In *Rhyssa* and in bees these muscles are represented by a single pair of internal ventral muscles. These muscles are absent in *Vespula* and *Dorylus*.

20. External ventral muscles of the second abdominal segment functioning as contractors of the abdomen in *Urocerus* and bees. These muscles are absent in *Rhyssa*, *Vespula* and *Dorylus*.

21. Reversed external ventral muscles of the second abdominal segment functioning as extensors of the abdomen in *Urocerus*, the honey-bee and *Vespula*. These muscles are absent in *Rhyssa*, *Bombus* and *Dorylus*.

22. Indirect wing depressor muscles (fig. 6D).

23. Retractor muscles of the mesothoracic postphragma of Apocrita. These muscles arise on a median and posterior projection of the propodeal tergum of bees and on the anterior surfaces of the propodeal prephragmata of *Rhyssa*, *Vespula* and *Dorylus*.

24. Reversed external lateral muscles of the third abdominal segment of *Bombus*.

25. Internal ventral muscles of the third abdominal segment of *Vespula* and *Dorylus* functioning as contractors of the abdomen.

26. External ventral muscles of the third abdominal segment of *Vespula* and *Dorylus* functioning as contractors of the abdomen.

27. Reversed external ventral muscles of the third abdominal segment of *Vespula* and *Dorylus* which function as extensors of the abdomen.

28. Median internal dorsal muscles of the third abdominal segment of *Dorylus* functioning as tergal retractors.

29. Oblique lateral dorsal muscles of the third abdominal segment of *Dorylus* functioning as tergal retractors.

30. External dorsal muscles of the third abdominal segment of *Dorylus* functioning as extensors of the abdomen.

VII. Abbreviations Used on the Figures

a2, *a3*, anterior apodemes of second and third abdominal sterna.
acs2, *acs3*, antecosta of second and third abdominal sterna.
act2, *act3*, antecosta of second and third abdominal terga.
a3, *l3*, and *a4*, *l4*, fused anterior and lateral apodemes of third and fourth abdominal sterna.
as1, *as2*, *as3*, *as4*, sterna of first, second, third and fourth abdominal segments.
at1, *at2*, *at3*, *at4*, terga of first, second, third and fourth abdominal segments.
d, dorsal intersegmental muscle.
d3, dorsal intersegmental muscle of metathorax.
e, dome-like region of membrane on dorsal surface of petiole of Apocrita.
e3, endosternum of metathorax.
e2, *3*, fused endosterna of mesothorax and metathorax of bees.
ep, epimeron of metathorax.
es, episternum of metathorax.
hw, hind wing.
l2, *l3*, lateral apodemes of second and third abdominal sterna.
ls, socket of hind leg.
m, membrane.
mc, coxa of hind leg.
mt, metathoracic tergum.
n3, metanotum.
p3, metapleuron.
ph3, prephragma of propodeum.
pn3, postnotum of metathorax.
r, median ridge of second abdominal tergum of Apocrita.
rg2, ridges on lateral edges of second abdominal sternum in *Vespula* and on lateral edges of sternum and ventral edges of tergum in *Dorylus*.
rg3, ridges on lateral edges of third abdominal sternum and on ventral edges of tergum in *Dorylus*.
s1, *s2*, *s3*, spiracles of first, second and third abdominal segments.
sr, part of propodeal orifice which forms a socket for ridge *r* in Apocrita.
t, tongue-like projection from first abdominal tergum fitting beneath metathoracic epimeron in *Urocerus*.
tr, tooth-like projections from propodeal tergum into propodeal orifice which articulate with lateral surfaces of ridge *r* in Apocrita.
ts3, metasternum.
v, small crescentic depressions on lateral edges of second abdominal sternum in *Urocerus*. The tergo-sternal muscles 12 insert on the internal ridges of these depressions.
ve, ventral intersegmental muscle.

w, oval projections on lateral edges of second abdominal sternum in *Urocerus*. The tergo-sternal muscles 13 insert on these projections.

x, small crescentic sclerotisations in membrane of lateral parts of first abdominal sternum in *Urocerus*. The tergo-sternal muscles 4 insert on these sclerotisations.

y, small circular ridges on dorsolateral parts of first abdominal tergum in *Urocerus*. These ridges enclose areas on which the tergo-sternal muscles 4 have origin.

z, small, well sclerotised circular regions on dorsolateral parts of second abdominal tergum in *Urocerus*. The tergo-sternal muscles 12 have origin on these regions.

2ph, mesothoracic postphragma.

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